

FIVE NEW SPECIES OF BATHYAL ATLANTIC ASCOTHORACIDA (CRUSTACEA: MAXILLOPODA) FROM THE EQUATOR TO 50° N LATITUDE

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ABSTRACT

Five new species of Ascothoracida are described from the Atlantic Ocean at depths of 700–3,500 m: *Synagoga paucisetosa* new species, host unknown, from 3,459 m in the equatorial Atlantic, based on a male; *Synagoga bisetosa* new species, host unknown, from about 2,000 m outside the Strait of Gibraltar, based on an immature ♀ female; *Thalassomembracis atlanticus* new species, host *Chrysogorgia quadriplex* Thomson, from about 1,450 m SW of the British Isles, based on a female; *Zoanthoecus scrobisaccus* new species, host *Epizoanthus satuu* (M. Schultze), from 927 m near the Azores, based on females, a male, and nauplii; *Dendrogaster deformator* new species, host *Novodinia antillensis* (A. H. Clark), from 711 m in the Bahamas, based on females. New specimens of *Cardomanica longispinata* (Grygier), host *Chrysogorgia elegans* (Verrill), are recorded from the Lesser Antilles. Both new species of *Synagoga* have a pair of *Waginella*-like pits on the front inner surfaces of the carapace valves. *Synagoga bisetosa* has a unique thoracopod segmentation and is intermediate between other *Synagoga* species and *Waginella* in some features. Fouling organisms associated with some specimens of *Cardomanica longispinata* bring into question the nature of the relationship with the host. Naupliar antennule segmentation in *Zoanthoecus scrobisaccus* seems to be different from that of other ascothoracidans, with implications for maxillopodan systematics. *Dendrogaster deformator* is morphologically and ecologically intermediate between other species of *Dendrogaster* and the closely related genus *Bifurgaster*.

Compared to the Indo-Pacific region, the Atlantic Ocean outside the boreal and austral regions has very few records of Ascothoracida, a superorder of parasitic maxillopodan crustaceans that infest anthozoans and echinoderms. At bathyal depths in particular (200–4,000 m), where this group is generally most diverse, there are described from this region only one species of *Thalassomembracis* and two of *Cardomanica* from chrysogorgiid gorgonians (Grygier, 1984a; Lowry, 1985), one species each of *Isidascus* from an isidid gorgonian (Moyse, 1983) and of *Laura* from an encrusting zoanthid (Grygier, 1985a), one species of *Petrarca* from two ahermatypic corals (Grygier, 1985b; Zibrowius and Grygier, 1985), one named and one unidentified form of *Ascothorax* from ophiuroid hosts (Grygier, 1983b), and an unidentified larva (Grygier, 1988b). Examination of museum collections of crustaceans and potential ascothoracid hosts as well as the generosity of alert colleagues have provided me with diverse material representing five new and one previously described species of bathyal Atlantic Ascothoracida, distributed between the equator and 50°N latitude. These are described here.

METHODS

Most specimens were discovered upon visual inspection of their hosts, owing to a characteristic appearance or gallicolous habit. The two specimens of *Synagoga* were not attached to any host and had been misidentified by sorters as an ostracod and a cirriped cypris larva. After general examination, one valve or the entire carapace was removed from the main bodies of specimens to be examined in detail, usually as whole mounts in glycerine. Dissected appendages and sometimes parts of carapaces were mounted unstained in glycerine jelly. Drawings were

mostly made with the help of drawing tubes on various dissecting and compound microscopes (standard optics and phase contrast); Fig. 5A was traced from a photocopy of the entire specimen.

SYSTEMATIC SECTION

Superorder Ascothoracida Lacaze-Duthiers, 1880
Order Laurida Grygier, 1987b

Family Synagogidae Gruvel, 1905

Genus *Synagoga* Norman, 1888

Synagoga paucisetosa new species

Figure 1, Table 1

Material.—Holotype ♂ (National Museum of Natural History Cat. no. USNM 228266), ATLANTIS II Cruise 31, sta. 156, central equatorial Atlantic (14-II-1967, 0°46.0'–46.5'S, 29°28.0'–24.0'W, 3,459 m). Host unknown.

Diagnosis (♂).—Carapace elliptical, about 2 mm long with anterior pit on inner face of each valve. Two spine-like setae on fourth antennular segment slightly unequal, armed with small denticles; few setae on fifth segment. Thoracopodal endopods armed only with 2 distal setae; many short setae on lateral edge of first exopod segment in thoracopods 2–4. Telsonic spines over half as long as furcal rami, extending beyond end of latter's ventral spine row; few medial furcal setae.

Etymology.—Named for the paucity of antennular, furcal, and especially medial thoracopodal setae.

Description.—Carapace bivalved with short dorsal hinge, lenticular, elliptical in side view except for slight anterodorsal protrusion, 2.04 mm long, 1.64 mm high, about 0.72 mm wide (Fig. 1A). Outer surface with scattered pores, dense band of similar pores along inner margin of each valve. Submarginal guard setae anteriorly and posteriorly, also row of cuticular ctenae posteriorly and posteroventrally. Pair of tapered, blindly ending pits with radially striated internal structure opening on anterior inner surface of valves anterolateral to antennule bases; pits about 127 μm deep, mouths about 48 μm in diameter. Within valves, anterior and posterior gut diverticula forming rounded W, diverticula of testis parallel to them but shorter, forming inverted Y.

Body completely enclosed; in retracted position, tips of natatory setae of furca and thoracopods reaching valve margins (Fig. 1A). Anterodorsal cephalic attachment zone extending ventrally to include carapace adductor muscle. Head with pair of large, grasping antennules, pair of plumose sensory organs referred to as frontal filament complexes (not illustrated), and oral cone. Thorax 6-segmented, first segment clearly divided from head dorsally, first 4 thoracomeses alike, last 2 longer and not as high, sixth with pair of flap-like, lateral epaulets. Six pairs of biramous thoracopods. Abdomen 5-segmented, strongly curved, segments 2, 5, 1, 3, and 4 listed in decreasing order of length. First segment with posteroventral penis, fifth (telson) with pair of posteroventral spines and large, blade-like furcal rami.

Antennules 6-segmented, very large, raptorial in form (Fig. 1A). First and third segments triangular, latter with fine hairs along anterior margin, second segment oblong. Fourth segment very short, with short tooth distal to 2 long, spine-like setae on anterior side, proximal seta a little longer, both with denticles on distally-facing side. Fifth segment long, tapered, with curved posterior margin and 3 setae on anterior margin, 2 of them on short, proximal part set at distinct angle to rest of margin. Sixth segment longest, almost as long as oral cone if terminal claw included, clavate with narrow base. Movable claw with fringe of extremely short spinules along part of inner curvature (Fig. 1A, detail); 3 setae proximal to claw,

of which lateral one longer than medial; claw guard narrow, with lateral flange and 4 distal setae, 1 before and 3 behind apical hood; proximal sensory process at base of segment, with long, basally arising aesthetasc and 2 short and 1 long terminal setae.

Frontal filament complex with 2 rami, posterior one 0.46 mm long, ventral one 0.36 mm long with lobe-like basal appendix, both rami plumose with large numbers of 0.24 mm long aesthetascs arising along most of length (not illustrated, but similar to one shown in Fig. 2A).

Oral cone narrowly triangular in side view, length 0.62 mm, basal depth 0.27 mm, no setae on anterior side (Fig. 1A). Mouthparts appearing typical of genus in whole mount, not dissected for detailed examination.

Thoracopods approximately equal in length (first and sixth slightly shorter), reaching ventrally as far as tip of oral cone and to telson (Fig. 1A). Coxa long, slender, usually tapered, but cylindrical in thoracopods 1 and 6; basis also slender, shorter than coxa. Both rami of thoracopod 1 2-segmented, one ramus nearly twice as long as other (Fig. 1B), long ramus assumed to be exopod by comparison to other species, but *in situ*, short ramus found laterally on right limb (Fig. 1A), medially on left one. Exopods of thoracopods 2–5 2-segmented, proximal segment longer and thicker than distal one; endopods thinner than exopods, first 2 segments combined as long as first exopodal segment, third half as long as second exopodal segment (Fig. 1C–E). In thoracopod 6 both rami 2-segmented, equal in length but endopod thinner, 2 segments of each ramus equal (Fig. 1F). Many short setae along lateral edge of first exopodal segment in thoracopods 2–4, on thoracopod 2 arranged in about 10 proximal clumps and 18 more distal, single setae, on thoracopod 3 arranged in about 5 clumps of about 6 setae each (Fig. 1C), on thoracopod 4 about 20 setae altogether, but poorly displayed (Fig. 1D). Thoracopod 5 with ordinary fine hairs at this position (Fig. 1E). Marginal fine hairs present elsewhere on thoracopods but not systematically observed. Principal setation of right thoracopods given in Table 1; endopods of all limbs with terminal setae only. Most setae plumose, those of first thoracopod more densely so than rest and only about two-thirds as long (Fig. 1B versus 1C, E). No seminal receptacles, and no filamentary appendage at base of thoracopod 1.

Testis clearly visible within first thoracomere, with pair of sperm-filled vasa deferentia passing posteriorly into abdomen and thence into rami of penis (Fig. 1A). Penile shaft reaching midpoint of second abdominal segment, rami reaching beyond its end (Fig. 1G). Large anterior spine at distal end of shaft, rami thin, vermiform, armament not clearly seen in whole mount, but at least with a few distal setae.

Telsonic spines 0.35 mm long with row of dorsal spinules along basal half (Fig. 1A, detail).

Furcal rami 0.55 mm long, 0.10 mm high at base, tapering distally (Fig. 1A). Row of spines along proximal half of ventral edge (20 spines on right ramus, 19 on left), 3 long medial setae, 2 shorter terminal ones, 2 ventral setae of intermediate length, one arising at midlength, other at 80% of length, furcal setae setulose.

Remarks.—There are three previous records of *Synagoga*. Norman (1888; 1913) described *S. mira* from an antipatharian host in the Bay of Naples. Grygier (1983a) described *S. normani* from an alcyonacean host in East Africa, and later (1988b) recorded a supposed juvenile of this genus from plankton in the eastern Indian Ocean.

Similarities of *S. paucisetosa* to *S. mira* include the spinulation on the antennular claw and the type of spine-like setae on the fourth antennular segment, as

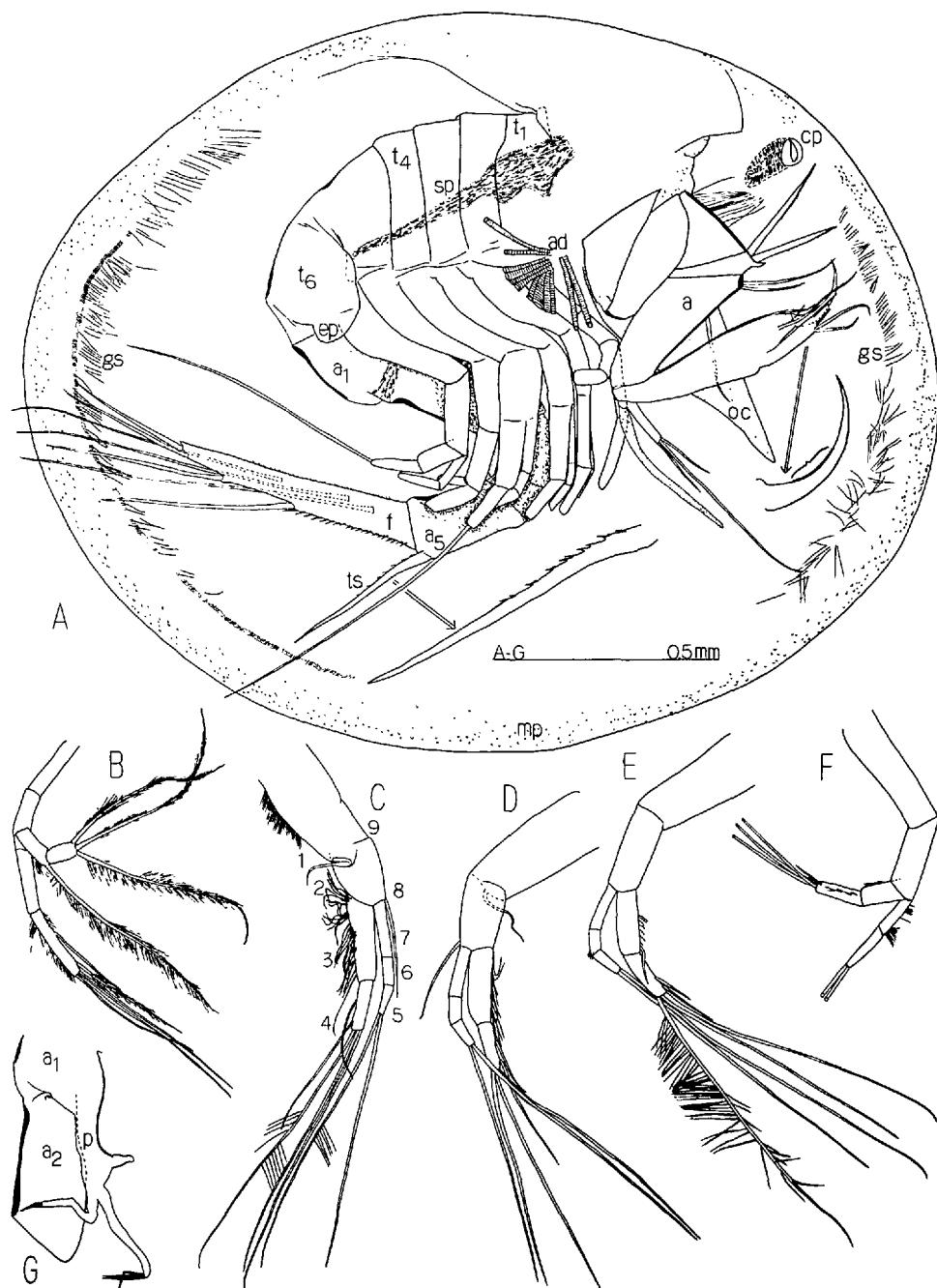


Figure 1. *Synagoga paucisetosa* new species, holotype ♂ (USNM 228266). A, habitus, right carapace valve removed, most thoracopodal setae and furcal setulation omitted, enlargements of antennular claw (fringe of spinules marked by bracket) and telsonic spine; B-F, right thoracopods 1, 3, 4, 5, and 6, respectively, representative setules shown on some setae, setae cut short in F, numbered regions in C corresponding to setal counts in Table 1; G, anterior part of abdomen with penis. Abbreviations for all figures: a, antennule; a_{1-5} , abdominal segments; ad, adductor muscle; ap, aperture; b_{1-4} , mantle branches; cg, claw guard; cp, carapace pit; dp, seminal receptacle duct papilla; ep, epaulet; f, furcal ramus; fa, filamentary appendage; ff, frontal filament complex; gd, gut diverticulum; gl, maxillary

Table 1. Thoracopodal setal counts of holotypes of three new species of Ascothoracida. Positions 1–9 are identified in Figs. 1C and 3D. Question marks indicate that the position in question was obscured, ranges indicate the extent of uncertainty about the true value. Parentheses are used for thoracopods with 2-segmented endopods. Short lateral setae in *Synagoga paucisetosa* and short medial setae in *S. bisetosa* are not included in the table. For position 4 in *S. bisetosa*, a+b+c refers to medial, terminal, and lateral positions, respectively, on the distal exopod segment

Species and limbs	Position on Limb								
	1	2	3	4	5	6	7	8	9
<i>Synagoga paucisetosa</i> new species, ♂, right									
1 (long ramus taken as exopod)	—	—	1	5	3	(—)	—	—	—
2	1	?	?	5	2	—	—	1	—
3	1	—	1?	5	2	—	—	1	—
4	1	—	0?	5	2	—	—	1	—
5	—	—	1	5	2	—	—	—	—
6	—	—	—	4	2	(—)	—	—	—
<i>Synagoga bisetosa</i> new species, immature, ♀, left									
1	—	—	—	5+3+2	2	(3)	2	1	—
2	1	—	—	6+3+3	2	(?)	?	2	—
3	—	—	1	6+3+4	2	(3)	4	3	—
4	1	—	—	7+3+3	2	(2)	4	3	—
5	—	—	—	6+3+1	1	(2)	4	2	—
6	—	—	—	4+3+0	1	(2)	3	—	—
<i>Thalassomembracis atlanticus</i> new species, ♀, left									
1	1	—	—	4	1	(—)	—	—	—
2	—	—	1	14	5	1	1	—	—
3	1	—	1	13–14	5	1	1	—	—
4	1	—	1	16	5	1	1	—	—
5	—	—	1	11	4	1	1	1	—
6	—	—	—	11	3	(1)	—	—	—

well as the penis structure (both species are known only from males). However, *S. paucisetosa* has many fewer setae on antennular segment 5 (3 versus 15), a much narrower proximal section of the sixth antennular segment, many fewer setae on the first thoracopod, nearly no medial setae on any thoracopods, and many fewer medial setae on the furcal rami (3 versus 10). The holotype of *S. paucisetosa* is within the size range of *S. mira* (2–4 mm), and, although its testes are not as extensively branched as those of *S. mira*, it appears to be sexually mature. Thus the setal differences are enough to justify recognition of a new species.

Synagoga paucisetosa is a little larger than the female holotype of *S. normani* (1.73 mm). Both have very few setae on antennular segment 5 and the medial faces of the furcal rami, a narrow protopod in thoracopod 1, and low exopodal setal counts on the thoracopods. Features of the present specimen which seem to warrant specific status include a different claw ornamentation (more widely spaced denticles in *S. normani*, not a fringe), dense arrays of lateral setae on the exopods

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gland swelling; gs, guard setae; h, holdfast; ip, isolated pouch; lb, labrum; m, middle piece; md, mandible; ml, medial languette; mp, marginal pores; mx₁, maxillule; mx₂, maxillae; oc, oral cone; oh, overhanging hood of first thoracomere; ov, ovary; p, penis; ps, proximal sensory process; r, rasp; rd, ridge; s, fusion seam; sl, spinose lobe; sr, seminal receptacle; sp, sperm; t_{1–6}, thoracomeres; th, thorax; ts, telsonic spine; vl, ventral lobe of thoracomere 6; vm, vestigial mouthpart.

of thoracopods 2–4, a near lack of medial thoracopodal setation, and much longer telsonic spines.

Grygier's (1988b) juvenile specimen is similar to *S. paucisetosa* in having 3 terminal and 1 penultimate setae on the endopod of thoracopod 1 (setal count of remaining limbs not obtained), few setae on antennular segment 5, and 3 medial setae on each furcal ramus, but the spine-like setae on antennular segment 4 in that juvenile are very unequal, the sixth antennular segment relatively much shorter and not clavate, the exopod of thoracopod 1 more setose, and the telsonic spines and furcal rami much shorter than in the new species.

None of the previously described forms of *Synagoga* has a pair of anterior pits on the inner surface of the carapace valves, or at least such structures were not noticed. Their significance will be discussed under *Synagoga bisetosa* new species below, which also has them.

Synagoga paucisetosa is the first representative of its genus from deep water (the capture depth of the Indian Ocean juvenile is unknown), and the first from the open Atlantic, although it shares both of these distributional characteristics with *S. bisetosa* new species. It does not bear any significant resemblance to *Waginella sandersi* (Newman) from the abyssal South Atlantic, which was originally described as a species of *Synagoga* (Newman, 1974).

***Synagoga bisetosa* new species**
Figures 2, 3, Table 1

Material.—Holotype, possibly immature ♀, preparing to molt (Muséum National d'Histoire Naturelle, Paris, Cat. no. Ci2044), Campagne Balgim 1984, CRYOS sta. CP68, outside of the Strait of Gibraltar (5-VI-1984, 35°11.9'N, 7°52.6'W, 1,998–2,077 m), host unknown.

Diagnosis.—Carapace elliptical, long axis about 3 mm, anterior pit on inner surface of each valve. Two large, hirsute, not spine-like setae on fourth antennular segment, aesthetasc of proximal sensory process arising terminally. Endopods of thoracopods 2–5 2-segmented; no more than 3 medial setae on coxae, multitudes of short setae medially on basis and first endopod segment of thoracopods 2–5, at most 3 longer setae on first endopod segment, most limbs lacking setae on first exopodal segment. Telsonic spines short. Furcal rami with 1 ventral and 3 terminal setae, more than 10 medial setae, spines in ventral spine row mostly subdivided.

Etymology.—Named for the 2 ordinary setae instead of spine-like ones on the fourth antennular segment, as well as for the single pair of ventral setae on the furcal rami.

Description.—Carapace bivalved with short, anterodorsal hinge, elliptical, lenticular, 2.8 mm high, 2.2 mm long, 1.0 mm wide, long axis apparently dorso-ventral (Fig. 2A). Outer surface finely pitted with pore openings. Inner surface with scattered long setae and submarginal band of spinules and guard setae, spinules forming comb-row around most of circumference, fused into stout clumps posterodorsally, setae most abundant anteroventrally and dorsally, longer but more widely spaced posterodorsally. Pair of tapered, bluntly ending pits with radially striated internal structure opening onto anterior inner surface of valves anterolateral to antennule bases (Fig. 1A, B); pits about 110 μm deep, mouths 48 μm in diameter. Gut diverticulum in each valve shaped like rounded W, with 3–4 short, ventral branches from each of main anterior and posterior branches.

Main body enclosed by valves except for furcal rami (Fig. 2A). Head attached to carapace anterodorsally, large adductor muscle present. Head bearing pair of large, grasping antennules, pair of plumose frontal filament complexes, and oral

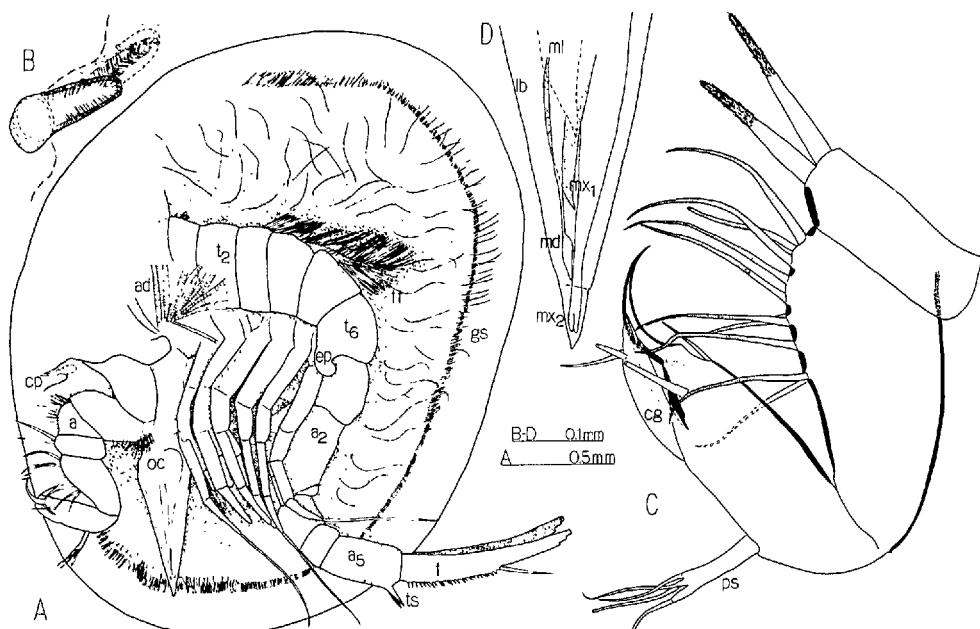


Figure 2. *Synagoga bisetosa* new species, holotype immature ♀ (MNHN Ci2044). A, habitus, left carapace value removed except at very front, most thoracopodal and furcal setae omitted; B, anterior carapace pits, nature of radial striation unknown; C, distal part of antennule, segments 4–6; D, distal half of oral cone showing mouthparts within. For abbreviations, see Fig. 1.

cone. Thorax 6-segmented, anterior border of first segment indistinct, few dorsal hairs on that segment. Thoracomeres unmodified, becoming slightly longer and less high towards rear; pair of large epaulets on sixth segment. Six pairs of biramous thoracopods. Abdomen 5-segmented, segments 2 and 5 longest, segments 1, 3, and 4 successively shorter. First segment with posteroventral penis, fifth (telson) with pair of posteroventral spines and furcal rami.

Antennules 6-segmented, folded in W-configuration (Fig. 2A, C). First 2 and last 2 segments all similar in size, middle 2 much shorter, segment 4 triangular. Dense, fine hairs on posterior margin of segment 2 and anterior margin of segment 3. Segment 4 with 2 large, slightly unequal setae, distal halves hirsute. Fifth segment with 10 long setae (on left antennule) divided into smooth shaft and corrugated or slitted distal part. Sixth segment with slender, movable claw armed on inner side with extremely tiny denticles; due to adhering debris, setation of this segment difficult to ascertain: 1 seta at base of claw, another lateral to it, possibly shorter one medially; claw guard with lateral flange and at least 3 distal setae, 1 before and 2 behind apical hood; proximal sensory process well separated from claw guard, with 3 terminal setae and slightly shorter, also terminal, stalked aesthetasc.

Frontal filament complex with 2 rami, ventral one 0.64 mm long, posterior one 0.99 mm long, both highly plumose with numerous cylindrical, blunt-tipped aesthetascs 0.24 mm long arising along most of length (part of posterior ramus seen in Fig. 2A); basal structures of ventral ramus not seen due to damage.

Oral cone narrowly triangular in side view, length 0.68 mm, basal depth 0.24 mm (Fig. 2A). Mandible harpoon-shaped, maxillule and medial languette pointed,

languette reaching to half free length of maxillule; maxillae bifid, longer than mandibles, posterior ramus at tip apparently not hook-like (Fig. 2D).

Thoracopods reaching ventrally to about two-thirds length of oral cone, or to third abdominal segment, equal in length except sixth slightly shorter (Fig. 1A). Each thoracopod with coxa, basis, and pair of 2-segmented rami, endopod as long as first exopodal segment (Fig. 3A–F). Coxa longer than wide, slightly tapered except cylindrical in sixth pair (suggestion of preoxa visible laterally at base of thoracopod 6; Fig. 3F), lined with fine hairs along both margins in thoracopods 2–5, laterally only in thoracopod 1. Basis rectangular, longer than wide, shorter than coxa, lateral edge generally bare (some short hairs in thoracopod 1) but sometimes with a few cuticular ctenae, medial edge with about 11 transverse rows of perhaps 3 short setae each in thoracopods 2–5. Exopod as long as protopod (slightly shorter in thoracopod 6), slender, first segment just over half of length. First segment bare in thoracopod 1, lined laterally with fine hairs in thoracopods 2–6, second segment with fine lateral hairs probably on all of thoracopods 2–6, but not seen in thoracopod 4. Proximal endopodal segment slightly shorter than distal one (but much longer than it in thoracopod 1), medially armed like basis in thoracopods 2–5, with about 7–8 transverse rows of perhaps 2 short setae each; distal segment with fine medial hairs in thoracopod 6, some medial short proximal setae like those on basis in thoracopods 2–5, lateral fine hairs at least on thoracopods 2 and 3. Principal setation of left thoracopods given in Table 1; long setae on medial side of basis and first endopodal segment posterior to short setae mentioned above, most setae cited in Table 1 plumose except for those on lateral edge of distal exopodal segment. No seminal receptacles, nor any filamentary appendage at base of first thoracopod.

Penis reaching to end of second abdominal segment, divided into shaft with anterior terminal spine, short flexible region, and 2 veriform rami, each ending in pair of tiny setae (Fig. 3G).

Telsonic spines fairly short, with distally-pointing dorsal spinules (Fig. 3H).

Furcal rami (Fig. 3H) about 0.75 mm long, 0.18 mm high at base, tapering distally, with few hairs and distal spine dorsally, cuticular ctenae lateroventrally, ventral seta at about 60% of length of ramus, 3 distal setae arising in closely set steps, dorsal 2 of these simple, other one and ventral seta plumose. Thirteen medial, simple setae arising in diagonal row along most of length of ramus, spacing increasing distally, these setae reaching to ends of distal setae except for first few; first one reaching only to end of ventral seta. Ventral edge of ramus with 25 (left) or 27 (right) very sharp, generally subdivided spines.

Hyperparasites.—Two cryptoniscid isopods were found between the carapace valves.

Remarks.—This specimen agrees with the most recent definition of *Synagoga* (viz., Grygier, 1983a) in its general carapace morphology and antennular structure, mouthparts, lack of a laterodistal coxal seta on thoracopod 1, and tapered furcal rami. It differs from that diagnosis in having perhaps only 3 rather than 4 setae on the antennular claw guard (not clearly seen here), rather large epaulets, all thoracopodal endopods 2-segmented, and 1 ventral seta instead of 2 on each furcal ramus. Differences in setation from all the forms of *Synagoga* previously described (*S. mira*, *S. normani*, *S. paucisetosa* new species, juvenile from the Indian Ocean) involve the antennules and the medial sides of the thoracopods. All the others have spinose or dentate, spine-like setae on antennular segment 4, and they also have an aesthetasc arising at the base of the proximal sensory process instead of terminally. Only *S. paucisetosa* has anything like the great number of short setae

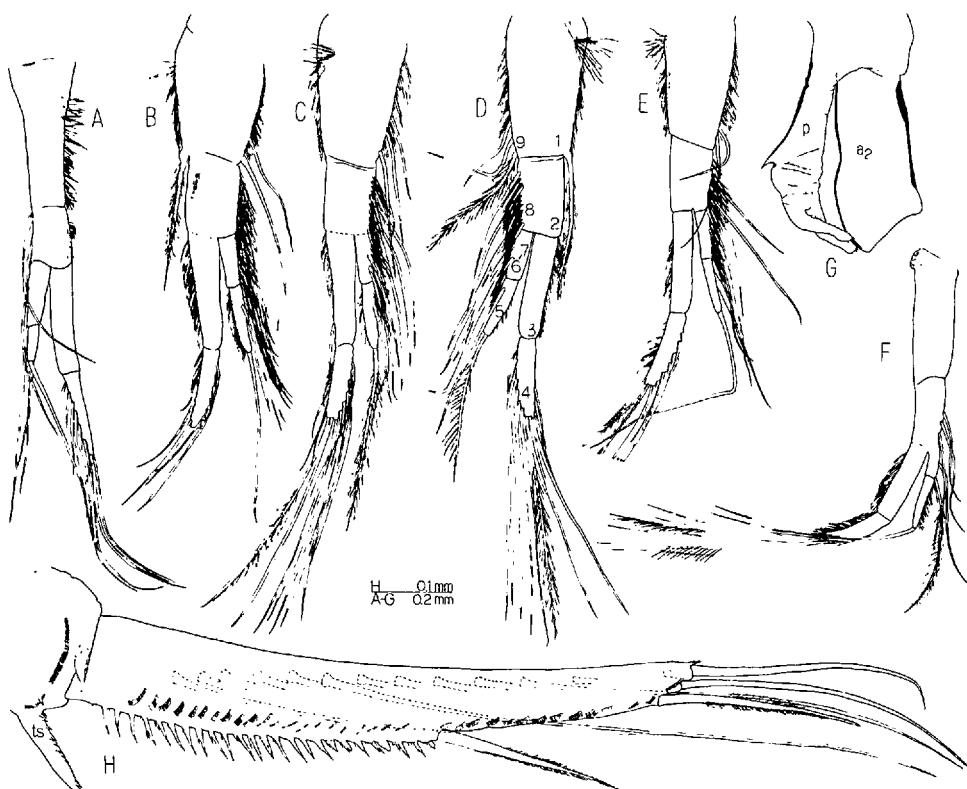


Figure 3. *Synagoga bisetosa* new species, holotype immature ♀ (MNHNP Ci2044). A–F, left thoracopods 1–6, respectively, long ramus of each is exopod, representative setulation shown on some natatory setae, exopodal setae cut short in E, longer exopodal setae omitted in B, numbered regions in D corresponding to setal counts in Table 1; G, anterior part of abdomen with penis; H, left furcal ramus and telsonic spine, bases only shown of most medial furcal setae. For abbreviations see Fig. 1.

found medially on the basis and endopod in *S. bisetosa*, but in that species they are found laterally on the first exopodal segment.

The present specimen falls between previous definitions of *Synagoga* and the related genus *Waginella* in some respects (Grygier, 1983a). Large epaulets are characteristic of *Waginella*, and in that genus all 4 marginal furcal setae are terminal, instead of 2 terminal and 2 ventral reported in *Synagoga* until now. *Waginella* also has carapace pits like the pair seen here and in *S. paucisetosa*, described above, but they open externally on the front end of the flattened ventral or anteroventral side of the valves. Such pits are absent from the juvenile *Synagoga* from the Indian Ocean (Grygier, 1988b) and have not been seen in *S. mira* or *S. normani*, although it is possible they were overlooked. They also occur externally on the anteroventral corners of the valves in males of both known species of the laurid *Zoanthoecus* (Grygier, 1985a; herein). The nature and function of these pits is unclear, but further speculation on their possible homology to the frontal horn pores of cirriped cypris larvae (Grygier, 1983a) will have to take into account their occurrence at two very distinct sites in the Ascothoracida.

Synagoga bisetosa is unique among generalized ascothoracids of all kinds in having uniformly 2-segmented thoracic endopods; in general the superorder is

characterized by 3-segmented endopods on thoracopods 2–5 (Grygier, 1987b). This, together with the other differences from previously known forms of *Synagoga* mentioned above, might readily justify a new genus for *S. bisetosa*. However, the only specimen is not sexually mature, and until more specimens are found, the possibility that the aberrant thoracopodal segmentation represents a developmental stage or even a deformity cannot be completely excluded. Phenetically this species' closest affinities are clearly with *Synagoga*, and it is therefore included in that genus for the time being, somewhat apart from the rest of the species.

Genus *Thalassomembracis* Grygier, 1984a

Thalassomembracis atlanticus new species

Figure 4, Table 1

Material.—Holotype ♀ (MNHN Cat. no. Ci986), "THALASSA" sta. Z452, SW end of Celtic Shelf (28-X-1973, 48°41.5'–39.0'N, 10°53.0'–55.2'W, 1,420–1,470 m), attached to colony of *Chrysogorgia quadriflex* Thomson. Brooding 500–505 oval eggs measuring 0.38 × 0.29 mm (mean of 12).

Diagnosis (♀).—Flat-sided carapace with dorsally rounded lateral profile, wide, rounded crest, and pair of blunt, anteroventral holdfasts; grapnels on holdfasts and along much of ventral margin, smaller papillae with usually 2 conical spines over rest of surface. Head with long, free dorsum, thoracomere 1 with pair of setose, transverse ridges, thoracomere 3 with transverse band of setae, thoracomeres 4–6 humped with transverse bands of setae. Antenular claw hirsute, 3 setae at its base, 3 setae on and 2 behind claw guard. Thoracopods with longer exopods than endopods; 1 seminal receptacle each in thoracopods 2–5. Small telsonic spines present. Furcal rami straight.

Etymology.—Named for the Atlantic Ocean.

Description.—Carapace length 3.90 mm ventrally, 4.36 mm from front to rear of dorsal brood chamber, height 4.47 mm, width 2.62 mm (Fig. 4A–C). In side view outline rounded dorsally, constricted at about one-quarter of height, somewhat convex ventrally. Flat sides diverging anterodorsally, then converging most of way around into wide, rounded crest. Vertical aperture on upper side of triangular, posteroventral protrusion (Fig. 4B), ventral margins tightly joined but separable as far forward as holdfast, small opening there for protrusion of tip of oral cone (Fig. 4C, D). Holdfast comprising pair of short, blunt, anteroventral processes 0.39 mm long, 0.59 mm thick (Fig. 4C, D). Typical *Thalassomembracis*-type grapnels, usually with 4 hooks, abundant on holdfast and anterior two-thirds of ventral margin, rest of carapace except near aperture set with much smaller papillae, usually bearing 2 (up to 4) radially pointing, conical spines. Gut diverticula consisting of at least 5 subdividing, radial branches, they and ovary diverticula restricted to flat part of carapace, not reaching into crest (Fig. 4D).

Body small relative to carapace, 2.9 mm from tip of oral cone to ends of furcal rami, 1.9 mm from tip of oral cone to top of ridges on thoracomere 1 (Fig. 4D). Vertical, anterior, cephalic attachment zone; extensive free dorsum of head anterior to aforementioned ridges, with pair of low, rounded lobes. Ventral side of head with antennules and oral cone, no frontal filaments found. Thorax 6-segmented, each segment with pair of biramous thoracopods, segments about equally long but decreasing in height posteriorly (Fig. 4D); first segment with pair of setalined, transverse ridges, third with transverse, dorsal band of setae, fourth through sixth humped with transverse bands of setae; bulbous lateral epaulets on sixth segment, 4 pairs of triangular sclerites above insertions of thoracopods 2–5. Abdomen 5-segmented, bent 90°, third and fourth segments shorter than others, first

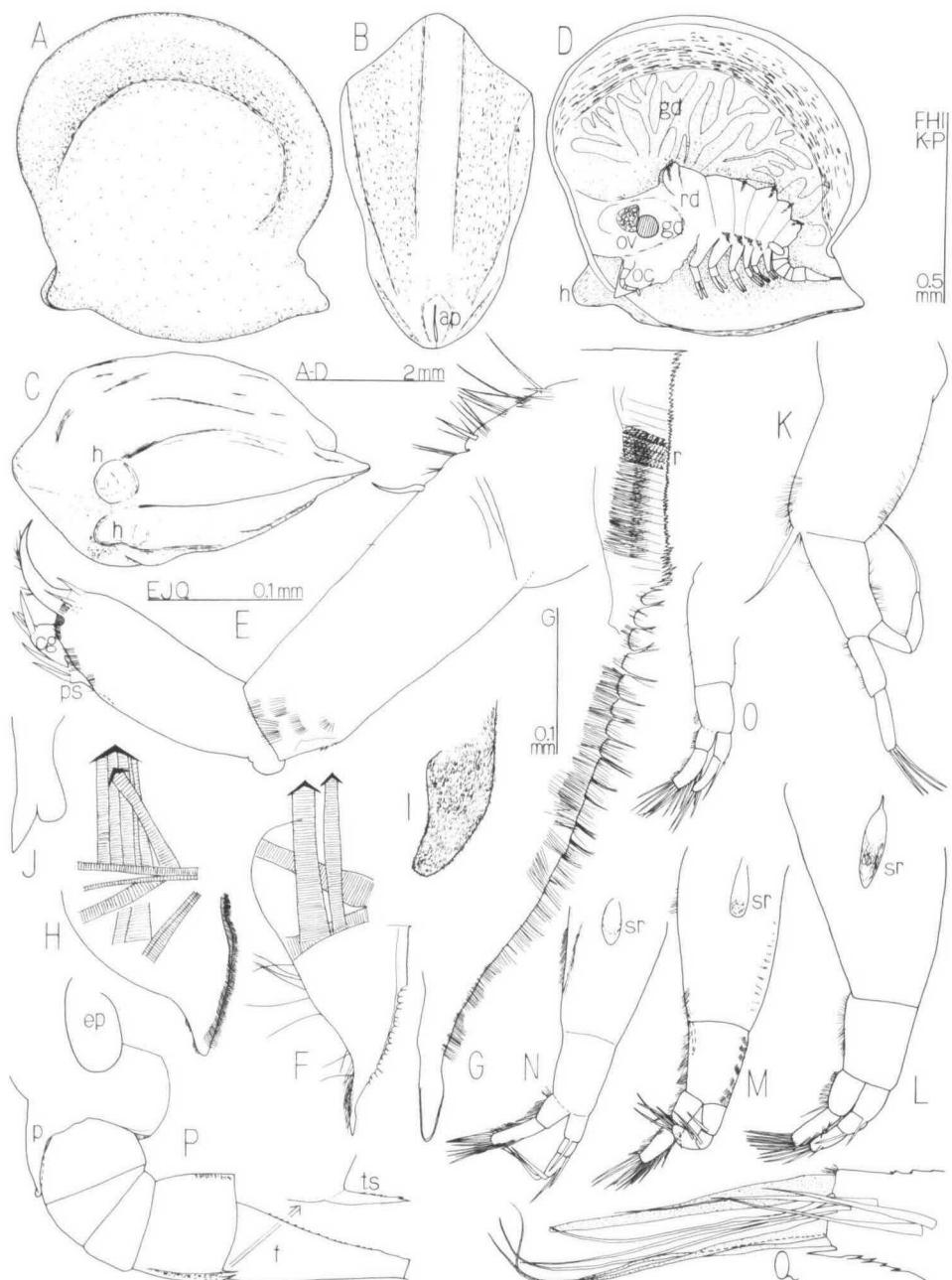


Figure 4. *Thalassomembracis atlanticus* new species, holotype ♂ (MNHN Ci986). A–C, lateral, posterior, and ventral views of carapace, respectively, anterior end left in A and C; D, habitus, left half of carapace removed, thoracopodal setae omitted; E, distal part of antennule, segments 4–6; F, mandible; G, medial edge of mandible, only part of rasp-like basal surface shown in detail; H, maxillule; I, medial languette; J, tip of maxilla; K–O, left thoracopods 1, 2, 4, 5, and 6, respectively, exopods on left, most cuticular ornamentation and marginal hairs as well as setal plumosity omitted; P, abdomen, left furcal ramus removed, furcal setae omitted, with detail of telsonic spine; Q, tip of left furcal ramus, medial view, 3 thick setae of posterior margin stippled, setules and 2 thin setae omitted. For abbreviations see Fig. 1.

with posteroventral penis, fifth (telson) with slightly roughened dorsal surface, small posteroventral spines, and furcal rami (Fig. 4P).

Antennules (Fig. 4E) about as long as oral cone (0.94 mm total length), 6-segmented, partly flexed, evenly tapered. Third and fourth segments shortest, third triangular, rest oblong. Fine hairs along anterior margins of segments 3, 4, and basally 5; 1 true seta distally on segment 4, another basally on segment 5. Cuticular ctenae distally on segment 5. Segment 6 with perhaps slightly movable, posteriorly hirsute claw, 3 setae at its base, stubby claw guard with 3 distal setae, 2 longer setae on low common base (proximal sensory process) behind it.

Oral cone nearly equilaterally triangular in side view (Fig. 4D), containing paired mandibles and maxillules, medial languette, and fused maxillae. Mandibles about 0.80 mm long, 0.43 mm wide across muscular base, sharply tapered distally (Fig. 4F); lateral edge with scattered hairs, becoming shorter and arranged into 2 rows distally. Medial edge of mandible 0.56 mm long and complexly armed (Fig. 4G): row of about 70 basal teeth, larger at either end; rasp-like surface of fine denticles on one side below this saw-edge, good correspondence between oblique rows of denticles and marginal teeth; many fine hairs in one or more comb-rows on opposite side from rasp; middle third of length with evenly spaced clumps of fairly thick hairs, finer marginal hairs scattered about, and submarginal comb-rows of fine hairs; fine, scattered hairs found farther distally, very tip obscured. Maxillules similar in shape to mandibles, but base equipped with more muscles and distal part shorter and blunter (Fig. 4H); medial edge with basal brush of fine hairs and then comb-row of setae; second, submarginal comb-row of longer setae also present, diverging farthest from margin near tip. Medial languette tongue-shaped in side view (Fig. 4I), triangular in cross-section, clothed in short, fine hairs. Maxillae massive, distally tapered, with blunt, bifid tips (Fig. 4J).

Thoracopods shorter towards rear (Fig. 4D, K–O), sixth only half as long as first. Slightly tapered coxa making up about half of length. Basis longer than wide, tapered. Exopods 2-segmented, distal segment little longer (difference greatest in thoracopod 6) except equal in thoracopod 1. Endopod 2-segmented in thoracopods 1 and 6, otherwise 3-segmented, little shorter than exopod, middle segment shortest in thoracopods 2–5, distal segment little longer than proximal in all thoracopods. Heavy raiment of marginal hairs (especially laterally) and cuticular ctenae (especially medially) on all thoracopods. Setal counts of left thoracopods given in Table 1; distal setae plumose (stiffer with shorter setules in thoracopod 1), shorter than rami. No filamentary appendage at base of thoracopod 1. Single oval seminal receptacle (120–210 μm long, 55 μm wide) with long duct located proximally in coxae of thoracopods 2–5 (Fig. 4L–N). Thoracopods with complete musculature (cf. Grygier, 1987c, fig. 7C) except lateral muscle to base of exopod not seen in thoracopods 4 and 5.

Penis tapered, uniramous, unarmed, reaching end of second abdominal segment (Fig. 4P). Telsonic spines with small spinules (Fig. 4P, detail). Furcal rami 0.46 mm long, basal height 0.20 mm, terminal height 0.06 mm, dorsal edge straight, basal half of ventral edge slightly convex, otherwise straight with terminal spine (Fig. 4P, Q). Many cuticular ctenae on faces. Ten distal, setulate setae, longest ones 40% as long as rami, 3 on distal edge (especially dorsal one) much thicker than remaining mediadistal ones (Fig. 4Q).

Remarks.—This species agrees with Grygier's (1984a) diagnosis of *Thalassomembracis* in having an anteroventral holdfast, grapnels, and radially toothed papillae on the carapace, a certain antennular setation and mouthpart morphology, setose humps on at least some thoracomeres, longer anterior thoracopods, large epaulets,

and a vestigial penis. It differs from any of the 6 previously described species in the long free dorsum of the head, the paired, hirsute ridges on the first thoracomere, the thoracic exopods longer than the endopods (contradicting the earlier generic diagnosis), the lack of lateral coxal setae on some of the first 5 thoracopods, and the straight dorsal margin of the furcal rami (upturned in other species).

The carapace form is most similar to *T. conquistador* Grygier, which also has a rounded dorsal profile in side view, a crest, and a bipartite holdfast. The high number of thoracopodal exopod setae is most similar to *T. acanthosphaericus* Grygier, and this species, along with *T. bayeri* Grygier and *T. orientalis* Grygier, also has transverse bands rather than tufts of dorsal thoracic setae. The latter 2 species are the only ones with radially toothed carapace papillae (but they do not have any grapsels) and with 1 rather than 2 seminal receptacles per thoracopod (some of the other species have just 1 in thoracopod 5). However, the seminal receptacles are rather specialized in these 2 species, with those of *T. orientalis* being more similar to those of *T. atlanticus*. For the moment, then, the affinities of *T. atlanticus* are ambiguous, but they may become clearer after a large number of new Indo-Pacific species of *Thalassomembracis* are described (Grygier, in prep.).

Genus Cardomanica Lowry, 1985
Cardomanica longispinata (Grygier, 1984a)

Isidascus longispinatus—Grygier, 1984a: 143, fig. 1A–C, E, G, fig. 2A–I, M, O–Q, table 1. Not Müller and Walossek, 1988, fig. 11S (= *Cardomanica quadricornuta* Lowry, 1985).

Cardomanica longispinata—Lowry, 1985: 322.

Material.—Two ♀♀ (USNM 228264) attached to base of colony of *Chrysogorgia elegans* (Verrill) (USNM 52865, Bayer #1679), R/V PILLSBURY sta. P-904, off St. Lucia, West Indies (9°VII-1969, 13°45.5'N, 61°05.7'W, 457 m). Three ♀♀ (USNM 228265) attached to bases of separate colonies of *C. elegans* (USNM 52858, Bayer #1680), R/V PILLSBURY sta. P-881, off St. Vincent, West Indies (6°VII-1969, 13°20.8'N, 61°02.5'W, 567–823 m).

Observations and Remarks.—All specimens attached to hosts in inverted position, grasping axis by means of sleeve formed by pair of anteroventral carapace protrusions. One specimen from sta. P-904 4.6 mm long, 4.2 mm high, other one 4.6 mm long, 3.5 mm high, 2.9 mm wide, with foraminiferan 1.5 mm in diameter firmly attached to right side of carapace. One specimen from sta. P-881 5.8 mm long, 4.5 mm high, another 5.3 mm long, 4.3 mm high, partly overgrown by nest of tubes (hydroid?), third not measured.

This species was originally reported from the Caribbean Sea off Colombia on *Chrysogorgia* sp., and from the Gulf of Mexico and the Bahamas on *C. elegans* and *C. cf. elegans*, respectively (Grygier, 1984a), but Lowry (1985) recognized the Bahamian specimen as a distinct species. The depths of occurrence in the Caribbean and Gulf were 366–531 m. The specimens from sta. P-904 are the same size as the holotype, while those from sta. P-881 are larger, but still considerably smaller than the Bahamian *C. quadricornuta*.

Some of the present specimens are associated with or actually a substrate for encrusting organisms. In all but one case there was no evidence of host tissue near the site of ascothoracid attachment (although this delicate tissue may have been lost in the trawl), and the sleeve joints are generally loose, allowing some movement and sometimes even free rotation around the axis. These facts cast doubt on whether *C. longispinata* is truly parasitic upon *Chrysogorgia*, or just using it as a substrate while feeding in another manner. This idea was first devised by Lowry in early drafts of his 1985 paper on *Cardomanica* from Australia, based on observations of the mode of attachment, but not of fouling organisms. How-

ever, following reviewers' comments, Lowry omitted this discussion from the published version of his paper. Lowry clearly had a valid point, and the problem of a possibly non-parasitic ascithoracidan bears investigation. Grygier (1981) suggested that the related synagoid *Gorgonolaureus muzikae* Grygier might be a barnacle-like filter feeder, but, as predicted by Moyse (1983), observations of living animals did not support this (Grygier, 1984b).

Family Lauridae Gruvel, 1905
Genus *Zoanthoecus* Grygier, 1985a

Zoanthoecus scrobisaccus new species
Figures 5, 6

Material.—Holotype ♀ and 16 paratype ♀♀ alive when captured, some of them brooding nauplii, 2 dead, non-type ♀♀, paratype ♂ accompanying holotype (all deposited in Musée Océanographique de Monaco), Prince Albert I^{er} sta. 105, Azores (25°VI-1887, 38°23'45"N, 28°31'15"W, 927 m). Host *Epizoanthus fatuus* (M. Schultz) overgrowing dead gorgonian (Cat. no. M0132026, in part). Non-type ♀ found on portion of same host from sta. 105, labelled as *Polythoa fatua*, in Zoological Institute, Academy of Sciences of the USSR, Leningrad.

Diagnosis (♀).—Carapace 5–8 mm high, length less than two-thirds height, width about 40% height. Radially bifurcating lateral furrows outlining isolated pouch near aperture protrusion and 2 series of radially directed marginal pouches on each side, 4 largest pouches with round excisions on edges. Thorax without distinct, short tergites, eave-like frill on front of first thoracopore, thoracomes 2–5 with elevated front ends; patches of dorsal setae on thoracomes 2–6 and first abdominal segment. Thoracopod 5 not more than vestigial lobe. Furcal rami twice as long as maximum height. ♂.—Carapace pits not in discrete papillae, penis lacking terminal setae, comb of blunt spines on rear margin of furcal rami.

Host-parasite Relations.—The parasites were evident as nodules or galls formed by accumulations of host polyps, which otherwise were widely spaced upon the gorgonian skeleton (Fig. 5A). Most galls held a single female parasite, but one double gall was found. The parasites within have the lateral side of the carapace appressed to the gorgonian axis and are held there and partly encapsulated by thin deposits of zoanthid secretion; the 2 dead specimens were completely coated. Pax and Müller (1956) studied part of the present material and noticed the nodules, but did not recognize them as parasites.

Etymology.—From Latin *scrobis* (furrow) and *soccus* (sac), referring to the laterally furrowed carapace.

Description.—Female: Carapace univalve, reniform, with lateral furrows, sizes of 7 specimens removed from host ranging from 5.3 mm high, 3.3 mm long to 7.9 mm high, 5.0 mm long, 3.3 mm wide (holotype 7.3 mm high, 4.8 mm long). In general, length 56–67% of height, width about 40% of height. Short, bulbous protrusion with vertical aperture located at midheight of posterior side, pair of lobes with thick cuticle and heavy spination flanking it ventrally (Fig. 6A). In lateral view each side of carapace divided by radiating pattern of deep, semi-enclosed troughs into many pouches pointing towards apertural protrusion, troughs terminating short of midline as round "pits" (Fig. 5B–D). Round, isolated pouch anteroventral to aperture protrusion, small marginal one dorsal to protrusion, usually 6 large, lanceolate, radial pouches, 4 longest of which possessing a few round notches, secondary series of smaller marginal pouches between these large ones. In one specimen, few pouches of third series developed. Pattern of pouches and troughs nearly symmetrical on both sides of carapace, but marginal "pits"



Figure 5. *Zoanthoecus scrobisaccus* new species (Musée Océanographique de Monaco). A, 10 paratype ♀ (white) and 2 dead ♀ (hatched) in situ in galls on *Epizoanthus fatuus* (M. Schultze)-overgrown gorgonian skeleton; B, C, F and rear of abdomen in E based on holotype ♀, D, E, H, and I on a paratype ♀, G on a different paratype ♀; B, C, carapace of holotype, left and right sides respectively, first series of marginal pouches marked by asterisks (*) in B; D, carapace with simplest lateral furrow pattern; E, thorax and abdomen of female, composite, thoracopods dissected away; F, first thoracomere showing eave-like hood; G, oral cone; H, mandibles and maxillule; I, tips of maxillae; J, paratype ♂, lateral view of carapace, with detail of anteroventral pit; K, paratype ♂, body; L, naupliar antennule with apparent segments numbered. For abbreviations see Fig. 1.

alternating, not in pairs. Simplest specimen with 10–11 marginal “pits” per side, most complex with 18, usually about 14 (holotype with 14 on right side, 16 on left). Simple, round or conical papillae near aperture, setose ridge dorsally on inside of aperture (Fig. 6A).

Body very small compared to carapace, in holotype 1.8 mm from front of first thoracomere to tip of furcal rami. Body consisting of head with antennules and oral cone, arched, 6-segmented thorax with thoracopods on first 5 segments, and curved, 4-segmented abdomen with penis on first segment and furcal rami on last (Fig. 5E). Front edges of thoracomeres 2–5 upraised, steep, especially in segments 3 and 4 (Fig. 5E), first segment well delineated from head dorsally and laterally, front edge produced into short eave overhanging head (Fig. 5F). Patch of dorsal setae on thoracomeres 2–6 and first abdominal segment (Fig. 5E). No distinct lateral chitinous ridge, although ventral edges of tergites usually evident, no obvious distinction between tergites and arthrodial membrane along thorax, although front dorsal ends of thoracomeres 3–6 with thicker cuticle than elsewhere. Most seminal receptacles located in ventral part of thorax rather than in thoracopods (Fig. 5E).

Antennules digitiform, with 3–4 poorly defined segments (Fig. 6B–D). Terminal armament generally including long seta (equivalent to aesthetasc of proximal sensory process) and spiniform process (equivalent to claw guard), latter sometimes with subsidiary spine; sometimes 1–2 other small spines or setae. No frontal filaments observed.

Mouthparts only seen well in one paratype. Labrum with short anterior face, slight spout, and longer, curved, posterior margins meeting distally behind maxillae; only maxillae protruding from spout (Fig. 5G). Mandibles narrow, pointed, with medial retrorse spinules (Fig. 5H). Maxillules very broad-based, distal part triangular, shorter and thicker than mandibles, with fine lateral hairs (Fig. 5H). Medial languette half as long as distal part of maxillule (not illustrated). Maxillae tapered, with short, claw-like, posterior hooks and small posterior spines at bases of distal prongs (Fig. 5I).

Thoracopods 1–5 all uniramous and unsegmented; medial ventral swelling on thoracomere 6 (Fig. 5E). First pair of thoracopods narrow, tapered, with 1–2 distal setae and large, irregularly oval, basal swelling (filamentary appendage or “plate-like organ”; Fig. 6E). Thoracopods 2 and 3 flat, leaf-like (Fig. 6F, G), former about twice as large as latter, both with 2–8 small, distal setae and round, flask-shaped seminal receptacles (4–9 in thoracopod 2, 1–5 in thoracopod 3), irregular papilla for seminal receptacle ducts at lateral base of thoracopods (not shown in illustrations). Thoracopod 4 much shorter and narrower than thoracopod 3, sometimes with distal narrowing suggestive of separate segment, 2–4 distal setae (Fig. 6H); no seminal receptacles, but duct papilla present. Thoracopod 5 as small, asetose but sometimes hairy knob (Fig. 6I), sometimes hard to find (possibly absent?).

Penis as blunt lobe with or without posterior fine hairs (Fig. 5E). Ventral side of fourth abdominal segment with cuticular ctenae, small telsonic spines sometimes present as such (Fig. 5E), sometimes as hairy knobs, sometimes absent. Furcal rami 2.1 times as long as high, longer along ventral margin than dorsal, both margins convex, distal height about half maximum height (Fig. 6J). Short cuticular ctenae overall, longer, spine-like ctenae ventrolaterally, sometimes distal ones isolated as single spines. Usually 4 thick, distally hirsute, terminal setae, ventral one shortest, but 3 setae and 1 spine observed on one occasion, setae lacking on both rami of another specimen (artefact?).

Male: Bivalved carapace 0.71 mm long, 0.41 mm high, with oblique, nearly

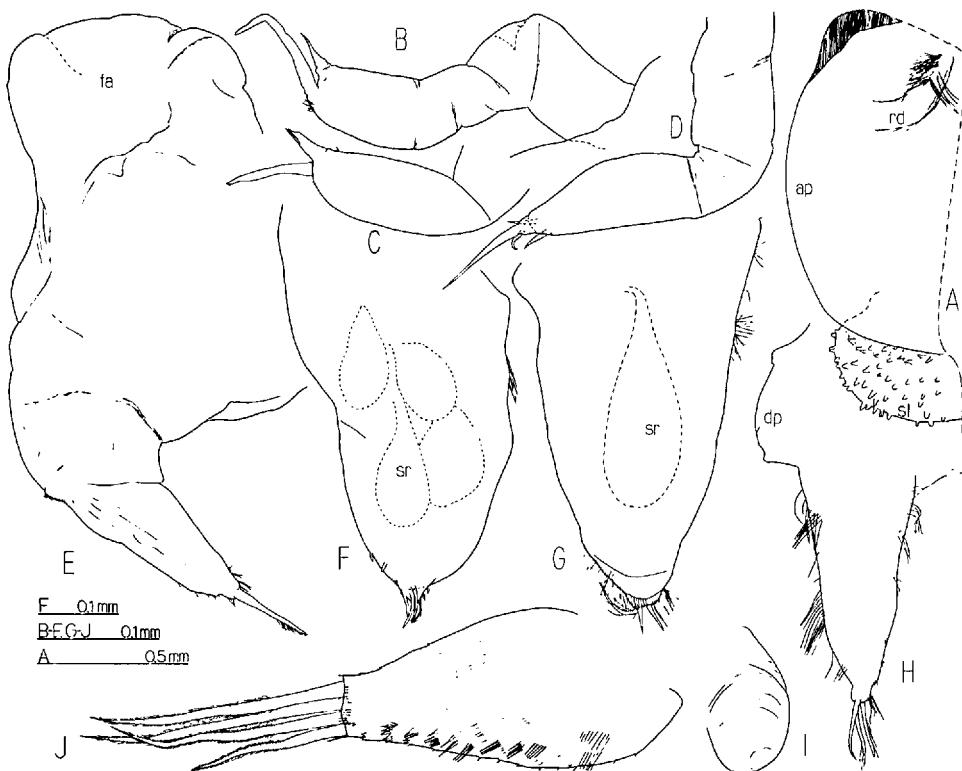


Figure 6. *Zoanthoecus scrobisaccus* new species (Musée Océanographique de Monaco). B, E, G–J based on holotype ♀, D on same specimen as Fig. 5D, A and C on same specimen as Fig. 5G, F on different paratype ♀; A, internal view of carapace aperture; B–D, antennules of 3 specimens, only distal part of C shown; E–I, thoracopods 1–5, respectively; J, right furcal ramus. For abbreviations see Fig. 1.

straight, posterodorsal margin, pair of blind pits on slightly protruding anteroventral corners (Fig. 6J, detail), and weakly developed, minutely spinose, surface ornamentation. Body completely enclosed, 0.42 mm from front of oral cone to tips of furcal rami (Fig. 6K). Head with oral cone and very large, raptorial-type antennules. Thorax 6-segmented, boundary with head not well displayed in preparation, segments becoming shorter and less high posteriorly, 6 pairs of thoracopods. Abdomen 4-segmented, sharply bent, with long, uniramous penis on first segment and furcal rami on last. Antennule with triangular first and third segments, oblong second segment, short fourth segment with 2 setae, tapered fifth segment with 2 basal setae; sixth segment with 3 setae at base of terminal claw, 2 short, distal setae on laterally flanged claw guard, and proximal sensory process well separated from claw guard, with seta and spinule on common base and separate, long aesthetasc. Oral cone equilaterally triangular in side view, with distinct spout. Protruding maxillae with blunt posterior hooks and very short distal prongs. No frontal filament seen. Thoracopods very slender, hairy, 6th only about 40% as long as 2nd, articulations poorly defined. Thoracopods 1 and 6 uniramous, 2–5 biramous (rami spiniform in thoracopod 5), exopods longer than endopods and obviously 2-segmented in thoracopods 2–4. Thoracopod 6 ending in long seta, single tiny seta each on exopods of thoracopods 2–4. Penis extremely long, but

only tip clearly seen, bearing distal flange but no setae. Telsonic spines small, simple. Furcal rami oblong, about 1.7 times longer than basal height, slightly tapered, with 4 ventral spines (including terminal one), comb of distal teeth along margin, and 4 terminal setae, ventral one shortest.

Instar I nauplii: Like those previously described for *Laura* spp. and *Zoanthoecus cerebroides* Grygier (1985a), only exceptional features cited here. Nauplii brooded by holotype 0.40 mm long, 0.23 mm wide (mean of 10). No frontal filaments or equatorial pores. Antennules apparently divided into 6 segments, with single medial seta on second and fourth segments instead of on adjacent segments as usual (Fig. 6L); this extra segmental division seen in 8 of 15 closely examined antennules from holotype brood, plus one from another brood. Antennal exopods with 5 setae and 8–9 segments, mandibular exopods with 4 setae and 7–8 segments, mandibular coxal endite sometimes with 1 spine, sometimes with 2.

Remarks.—One species of *Zoanthoecus* has been described until now, *Z. cerebroides* infesting the zoanthid *Gerardia* at 204–260 m on Nihoa Bank, Hawaiian Islands (Grygier, 1985a). That zoanthid also overgrows gorgonians, and the parasite also occurs in polypic nodules. The present species is assigned to *Zoanthoecus* primarily on the basis of the reniform carapace with lateral furrows, and secondarily by the anterior hood on the first thoracomere, the 5 pairs of thoracopods in the female, the "plate-like organ," and most of the seminal receptacles occurring in the thorax proper. Most of the other diagnostic features of this genus proposed by Grygier (1985a) prove to be only specifically diagnostic of *Z. cerebroides*.

The present females are larger (other species 2.1–5.8 mm high) and relatively thinner (in *Z. cerebroides* length 65–85% of height, width 45–65% of height), and have a more complex system of lateral furrows in most cases (only about 10 simple, rounded marginal pouches on each side in *Z. cerebroides*, no isolated pouch near the aperture protrusion). *Zoanthoecus scrobisaccus* lacks a large, transverse frill of arthrodial membrane between thoracomes 1 and 2, and also lacks unprotruded expanses of arthrodial membrane between the other thoracic segments. The dorsal thoracic setation is different; there are transverse bands of dorsal setae on thoracomere 6 and the first abdominal segment in *Z. cerebroides*, nothing farther anteriorly. There are up to 4 setae on thoracopod 1 in the *Z. cerebroides*, a better developed thoracopod 5, more seminal receptacles in the thoracopods, a longer penis, and relatively longer furcal rami (length 2.5–3.5 times height).

The present male is smaller than that of *Z. cerebroides* (latter 0.9 mm long), the anteroventral carapace pits do not open on discrete papillae, and the external carapace spination is relatively poorly developed. It also differs in having 2 equal (rather than unequal) setae each on antennular segments 4 and 5, 2 rather than 3 setae on the claw guard, a biramous thoracopod 5, and a longer thoracopod 6. Its penis lacks tiny distal setae found in *Z. cerebroides*, and the latter lacks a distal comb of spines on the furcal rami.

The antennules of the present nauplii have an indication of an extra segment between the 2 most proximal setae. Until now these setae have been held to arise on adjacent segments in the Ascothoracida (Grygier, 1987a), and the presence of an intercalary segment between them would have implications for maxillopodan systematics. Grygier (1987a) proposed setal homologies between the antennules of ascothoracidans, cirripeds, and facetotectans, and, using the setae as markers, further proposed segmental homologies. If the apparent extra segment in nauplii of *Z. scrobisaccus* is real, then the Ascothoracida could be considered to have a segment unaccounted for in the other groups. It could mean that the fundamental

number of antennular segments in the Ascothoracida is 9, not 8 as proposed by Grygier (1987a). Izawa (1987) expanded Grygier's analysis of antennules to include the Copepoda, Mystacocarida, and Cephalocarida. Mystacocaridans have a proximal cluster of setae on segment 3 and the next cluster on segment 5. These clusters are supposed to be homologous to the 2 proximal medial setae in ascothoracid nauplii; thus mystacocaridans have a possible homologue (segment 4) of the suspected extra segment in the present species. Before jumping to conclusions, however, confirmation is necessary in the form of similar ascothoracid nauplii, but of a later instar with clearly articulated segments.

Order Dendrogastrida Grygier, 1987b
 Family Dendrogastridae Gruvel, 1905
 Subfamily Dendrogastrinae Gruvel, 1905
 Genus *Dendrogaster* Knipovich, 1890

***Dendrogaster deformator* new species**

Figure 7

Material.—Holotype ♀ (USNM 235321) and smaller paratype ♀ (USNM 235322) removed from 2 interradial cysts of edge of disc of same specimen of brisingid asteroid *Novodinia antillensis* (A. H. Clark) (host deposited at Indian River Coastal Zone Museum), collected by J. E. Miller, R/V EDWIN LINK, dive JSL-I-1910, off Grand Bahama Island (28°X-1986, 26°25.20'N, 78°43.89'W, 711 m). Details of the association and a photograph of the infested starfish with the paratype alongside are given in Grygier (1988a). A color photograph of the living host *in situ* is given by Miller (1987: 47). Neither specimen brooding, no males found in dissected holotype.

Diagnosis (♀).—Maximum known size 11 mm. Mantle bilobed with 2–4 short, lobular side branches on each side, formed into spherical cluster totalling at most twice volume of short middle piece. No thoracic appendages. Antennules with 2 delicate setae on third segment, fusion seam and associated muscle in that segment, 3 setae on and 2 behind claw guard, 3 more at base of claw. Cysticolous in brisingid starfish.

Etymology.—Named for the parasites' deformation of the host asteroid.

Description.—Overall appearance as rounded clump of short, lobular branches with bent middle piece emerging anteriorly. Holotype (Fig. 7A) 10.9 mm long, 6.4–8.8 mm wide in different directions across mantle, middle piece about 7 mm long (bent at right angle at base), 4.1 mm thick, with distal, slit-like aperture. Paratype (Fig. 7B) 5.6 mm long, 4.1–4.9 mm wide in different directions across mantle, middle piece about 5.0 mm long (bent in 2 places), 2.7 mm thick, with distal, slit-like aperture. Behind middle piece, mantle consisting of 2 short, posterior lobes, each with 2 lobular side branches in paratype, 4 on one side and possibly both in holotype, side branches apparently all ending in 3 bumpy lobes. Color red when first removed from host, faded completely in alcohol.

Vestigial main body within tip of middle piece possessing antennules, oral cone, pair of posterolateral lobes presumably containing maxillary glands, and flat, posterior lobe presumably representing unsegmented, appendage-less thorax (Fig. 7C). Pair of gut diverticula leaving body anterodorsal to thorax, passing longitudinally down sides of middle piece.

Antennules 4-segmented, first segment triangular with very long baseline, second a parallelogram anteriorly recessed into first segment (Fig. 7D). Third segment an irregular quadrilateral longer than wide, rear margin slightly curved, anterior margin straight even beyond intersection with lateral fusion seam, muscle in anterobasal corner (Fig. 7E). Two extremely delicate setae observed at end of

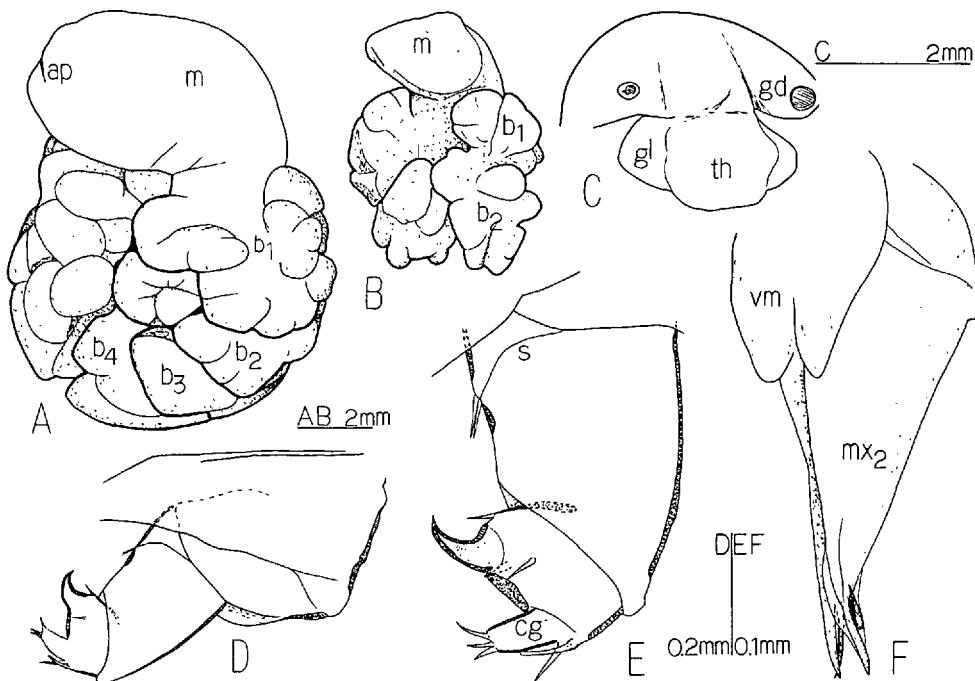


Figure 7. *Dendrogaster deformator* new species. A, holotype ♀ (USNM 235321), habitus; B, paratype ♀ (USNM 235322), habitus, branches artificially spread out; C-F from holotype; C, main body, posterior view, dorsal side of middle piece shown as curved line; D, antennule; E, distal antennular segments from D; F, mouthparts removed from oral cone. For abbreviations see Fig. 1.

fusion seam on one antennule, that region obscured in other. Fourth segment short, squat, partly recessed into anterior part of third segment. Strong, movable claw anterodistally, with 3 setae at its base, cylindrical claw guard posterodistally, with 3 terminal setae. Seta arising from thin cuticle at proximal base of claw guard, shorter aesthetasc on thickened base just behind it. Next instar's claw developing within present one.

Oral cone containing well developed maxillae and 1 pair of short, blunt, vestigial mouthparts, identity unclear (Fig. 7F). Maxillae tapering, tips bifid with movable, only slightly curved, posterior hooks.

Remarks.—This is the first record of adult *Dendrogaster* in the Western Atlantic between the Gulf of St. Lawrence and Patagonia. The very limited extent of the mantle branching is the most unusual feature of this species. Other species of *Dendrogaster* usually have an extensively branched carapace, most often with a pair of laterally directed main branches that split into long, subdividing, primary branches. There are a few species with a single pair of branches at the base of the middle piece (e.g., *D. astericola* Knipovich, *D. murmanensis* Wagin, *D. pontasteri* Stone, *D. asterinae* Achituv), but these branches always extend laterally, giving off either a few large processes or several fairly widely spaced side branches; none are similar to *D. deformator*. However, there is a certain resemblance between the new species and the other dendrogastrine genus, *Bifurgaster* Stone and Moyse (1985) (including *Paremedius* Stone, synonymized with *Bifurgaster* by Grygier (1987b)). In *Bifurgaster* a less well defined middle piece grades into a pair of

simple, thick, posterior lobes. If each lobe had side branches, the resulting effect would be similar to *D. deformator*. The cephalic appendages of both genera are essentially the same, and the antennular armament of the present species reflects the most common situation in both genera.

Dendrogaster deformator is the first species of its genus known to parasitize a brisingid starfish, and it represents one of the very few instances of *Dendrogaster* forming an externally visible cyst on its host (Grygier, 1988a). It is interesting, therefore, that *Bifurgaster* infests freyellid starfishes, very closely related to brisingids, and they caused marked swellings of the arm bases. Morphologically and ecologically, *D. deformator* seems to occupy an intermediate position between the two dendrogastrine genera. It is assigned to *Dendrogaster* on the basis of the mantle branches, few as they are.

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